Proc. Nat. Acad. Sci., India, 39(B), I & II, 1969

The Mouthparts and Feeding Mechanism of the Collembolan *Tomocerus longicornis* (Müller) (Tomoceridae)

By

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[Received on 20th March, 1968]

Our knowledge of the biology of Collembola, specially its feeding habits and the mechanism of food intake and digestion, is meagre and in certain respects erroneous. Folsom (1899) was the first to describe in some d tail the mouthparts of *Orchesella cincta*. He was followed by Hoffmann (1905, 1908 and 1911) who gave an account of the structure and musculature of mouthparts of *Tomocerus plumbeus* and drew attention to the rotatory movements of the mandible. He also described the nerve supply to the muscles in the head. Imms (1906) gave a brief account of the mouthparts of *Anurida maritima* and the structural similarities in the different Collembolan species. Denis (1928) studied the comparative anatomy of the head of *Anurida maritima*, *Onychiurus fimetarius* and *Tomocerus catalanus*, including the mandibular and maxillary musculature of the former two and the mandibular musculature of the last species, but his description of the origin and insertion of the muscles is superficial and incomplete. Recently Tuxen (1959) has described entognathy in apterygote insects from the evolutionery point of view and included the account of the Collembolan *Onychiurus armatus* and Manton (1964) has given an account of the mandibular mechanism of *Tomocerus longicornis* while discussing "mandibular mechanisms and evolution of Arthropods. Unfortunately none of these workers have studied the mouthparts and feeding mechanism and so the need for a comprehensive study of food, feeding habits and feeding mechanism in this Order is obvious. In the present series of papers the author has undertaken such a study in four species *viz. Tomocerus longicornis*, *Onychiurus armatus*, *Friesea mirabilis* and *Neanura muscorum*.

In the present paper the anatomy of the mouthparts of *Tomocerus longicornis* together with a description of the feeding mechanism has been given. It may be noted that this species occurs in leaf-litter and feeds on soft solid food (Singh, 1964 *a*, *b*; Poole, 1959).

Material and Methods

Specimens of *T. longicornis* were collected from the upper surface of the leaf litter of coniferous forest soil around Aberystwyth, U. K. They were also obtained from the decaying logs in a deciduous woodland from amongst mosses, at the base of bushes, ferns and undergrowth. For dissection purposes, they were fixed in hot Dubosq-Brasil fluid for three hours and then placed in 90% alcohol before being transferred to 50% lactic acid for twelve hours at 40°C for clearing. After this treatment, the mouthparts were clearly visible and were dissected out with fine needles and microscalpels made from safety razor blade. Permanent mounts of mouthparts were made in polyvinyl alcohol 'A' (Salmon, 1949) and lignin pink was employed as stain. The relationship of the muscles to the mouthparts was

studied under a phase contrast microscope. Further probing and dissecting, if necessary, were carried out with a Leitz micro-manipulator.

Details of the structure of the mouthparts and their associated musculature were elucidated from a study of serial sections. The head was fixed in Carnoy's fluid for 2½ hours at 40°C, cleared in Amyl acetate for atleast eight hours then placed in toluene for half an hour before transferring to paraffin wax with ceresin. (Steedman, 1960). For gross anatomical studies 4 to 15μ thick paraffin sections and 25μ thick celloidin sections, according to the method of Dennell (1940), were cut. Mallory's triple stain was mainly used for anatomical studies.

Observation and Discussion

A. The head and the arrangement of the mouthparts

The head of *T. longicornis* does not show segmentation. It is pear-shaped and slightly compressed dorso-ventrally. The head capsule is extended in the form of a cone at the end of which lies the opening of the pre-oral cavity. This is referred to as the hypostome. The mouthparts are prognathous and entognathous. They are enclosed in the cavity formed by the fusion of the lateral margins of the labium with the head (Folsom, 1900 ; Snodgrass, 1952). The cavity can be divided into two parts, the gnathal pouch which contains the posterior parts of the mandibles and maxillae and the pre-oral cavity which contains the hypopharynx and the anterior parts of the mandibles and maxillae. The free anterior parts of the mandibles lie above and parrallel to the hypopharynx, and their posterior parts or the shafts to which mandibular muscles are attached, lie suspended dorso-ventrally from the wall of the gnathal pouch by thin, flexible, folded, chitinous dorso-lateral ridge (*see* figs. 3 and 8) mesially, while the dorsal and ventral margins of the mandibular cavity continues as ample arthrodial membranes (fig. 9). The posterior end of each mandible is suspended from the lateral head wall by the mandibular suspension (fig. 1 and 3). The frame work of the maxilla lies parallel to the mandible. Its anterior part or head moves between the dorsal surface of the free part of the lingua and the ventral surface of the free part of the superlingua so that the fans on the maxilla head interlock with the longitudinal rows of bristles on the lingua and superlinguae. The posterior portion of the maxilla on which the muscles providing the motive force during feeding are inserted, lies in the gnathal pouch ventral to the mandible (fig. 8 and 9).

The hypopharynx occupies a median position in the pre-oral cavity (fig. 7). Posteriorly its dorsal surface forms the floor and sides of the cibarium and finally ends at the opening of the oesophagus. The space enclosed between the epipharynx dorsally and the labium ventrally is known as pre-oral cavity and opens to the exterior by a transverse opening. While feeding, the anterior parts of the mandibles, maxillae and hypopharynx can be protracted through the opening of the pre-oral cavity. This is a characteristic of entognathous insects.

The mouthparts and their musculature

Mandibles : Each mandible in *T. longicornis* is a stout structure modified for dealing with relatively larger food particles. Functionally it can be divided into two parts—an anterior part (anterior lobe) which lies free in the pre-oral cavity and is directly concerned with the manipulation of the food, and a posterior part (the shaft) to which are inserted the mandibular muscles. The incisor teeth are situated at the anterior end of the mandible and are used for scraping or cutting the food surface. These are of equal size and are arranged in a linear fashion. The right mandible has five incisors and lies slightly dorsal to the left mandible which has only four teeth. The molar plate (figs. 1 and 2) is a crescentric, curved

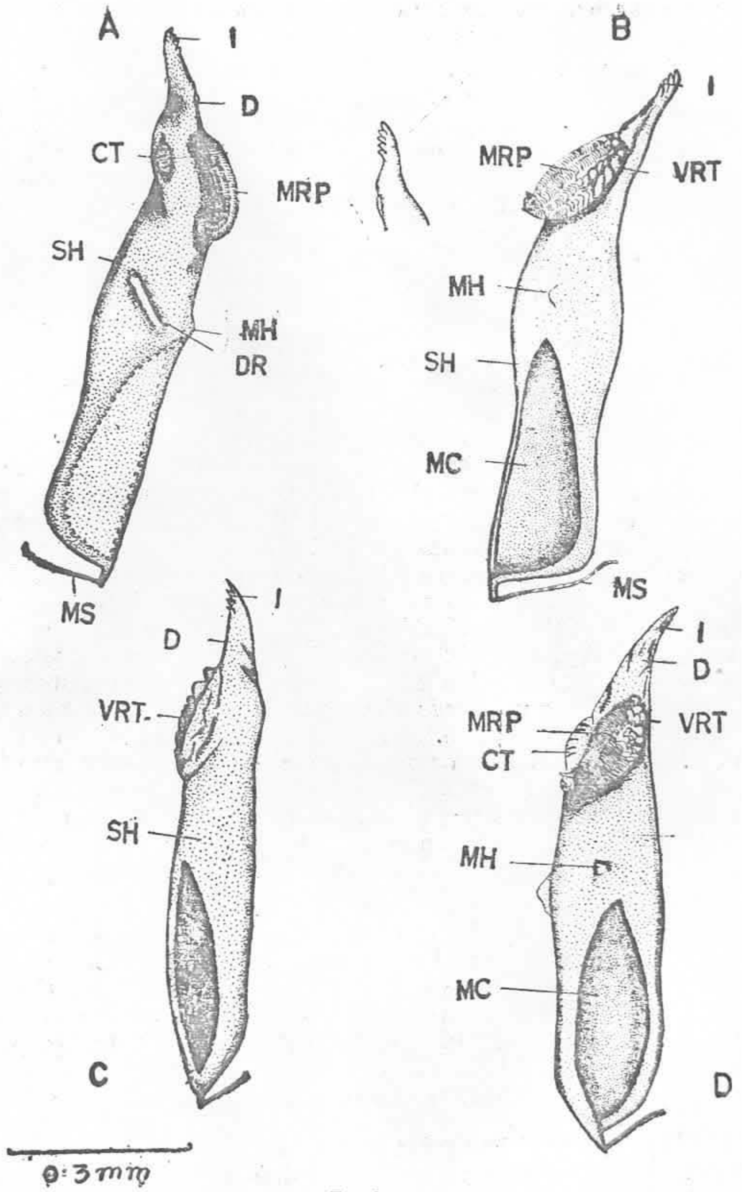

FIG. 1

Fig. 1. (*a*) Dorsal view of the left mandible.
(*b*) Dorsal view of the right mandible showing the five incisor teeth.
(*c*) Ventral view of the left mandible.
(*d*) Darso–lateral view of the left mandible.
(*e*) Mesial aspect of the left mandible.

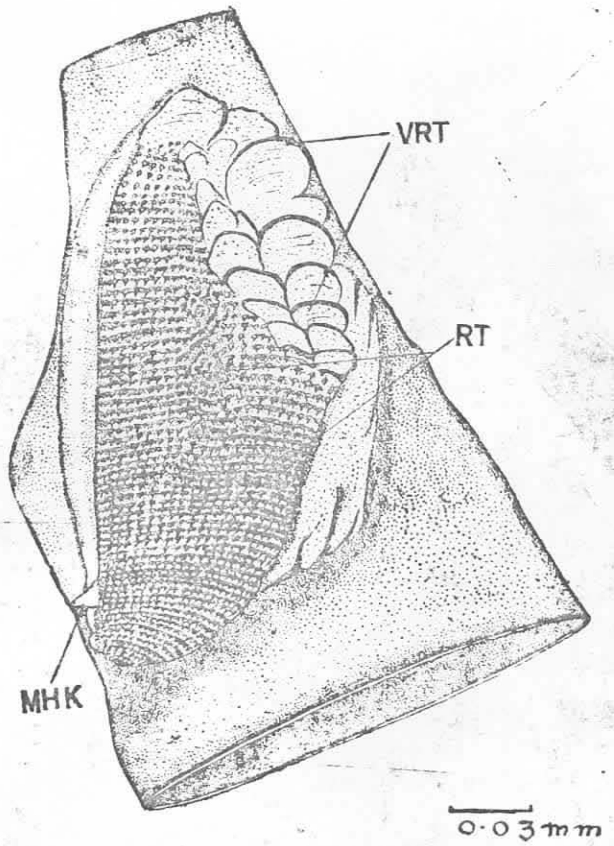

FIG. 2

Fig. 2. Mesial aspect of the molar plate of the left mandible of *T. longicornis.*

and convex area lying mesially on the anterior lobe of the mandibles. The crescentric shape of the molar plate follows the curved shape of the cibarium. The molar plates have a ventral region bearing large teeth which are arranged in two rows. Postero-dorsally there is a mandibular hook (fig. 2) which lies between the lateral folds of the epipharynx and the oral valve (figs. 7 and 6). The region of the molar plate between the hook and the ventral rows of the teeth is covered with teeth arranged in undulating transverse rows. (fig. 2).

The posterior part of the mandible is hollow and has been referred to as the mandibular cavity which opens mesially in a triangular fashion for allowing mandibular muscles to enter and insert.

The mandibles of *T. longicornis* show two types of movements—protraction which are accompanied by counter-rotation, and retraction combined with rotation. Rotation is a movement in which the molar surface of the mandible moves mesially and upward, whilst during counter-rotation it moves laterally and downward. The numbering of the musculatures used agrees with that of Manton (1964).

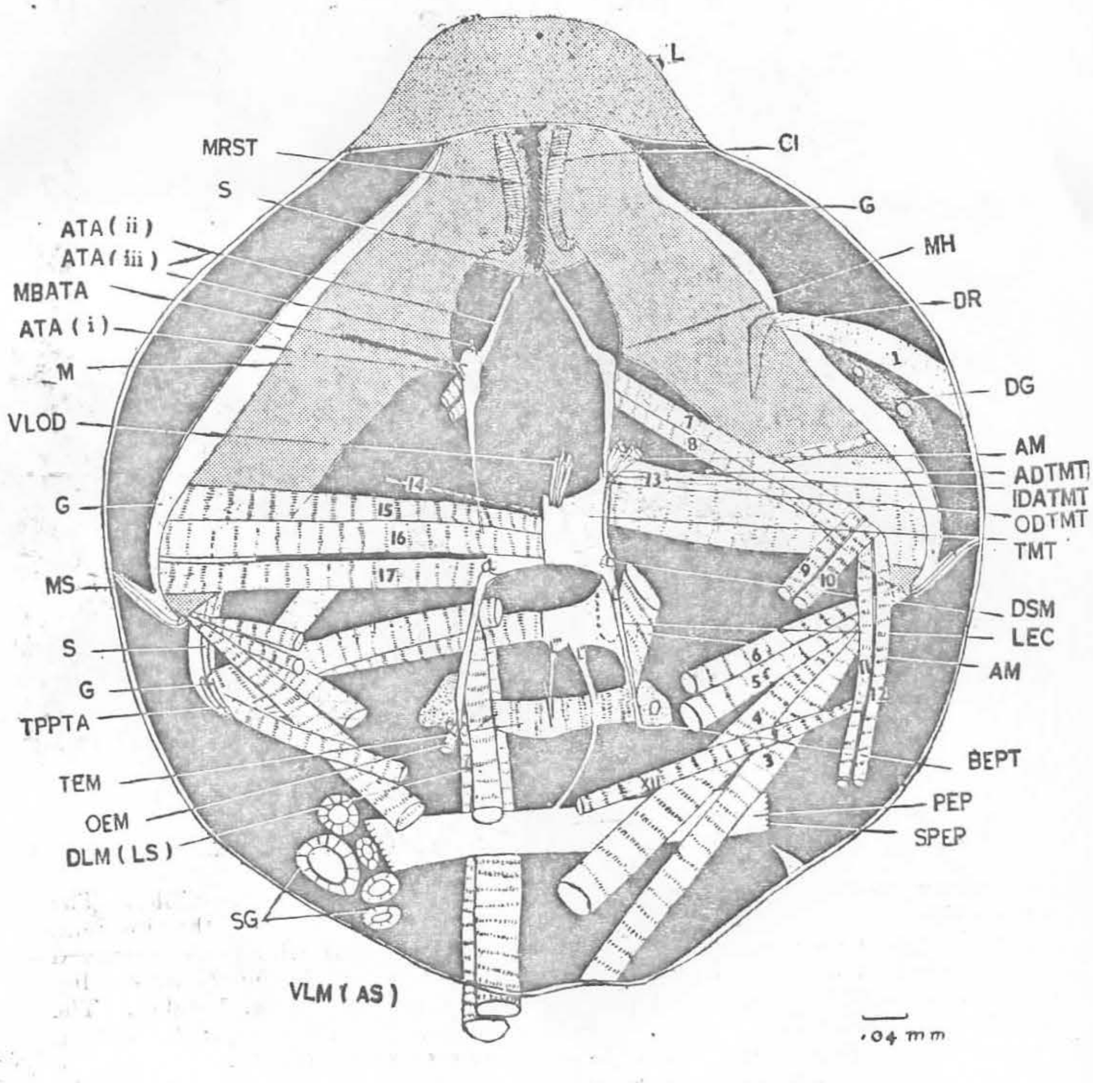

FIG. 3

Fig. 3. **Diagramatic horizontal section (reconstructed) of the head of *T. longicornis* showing the mandibular muscles viewed from above, the right side representing a more dorsal level than the left. Endoskeletal structures and maxillary muscles have been incorporated to show their relative positions.**

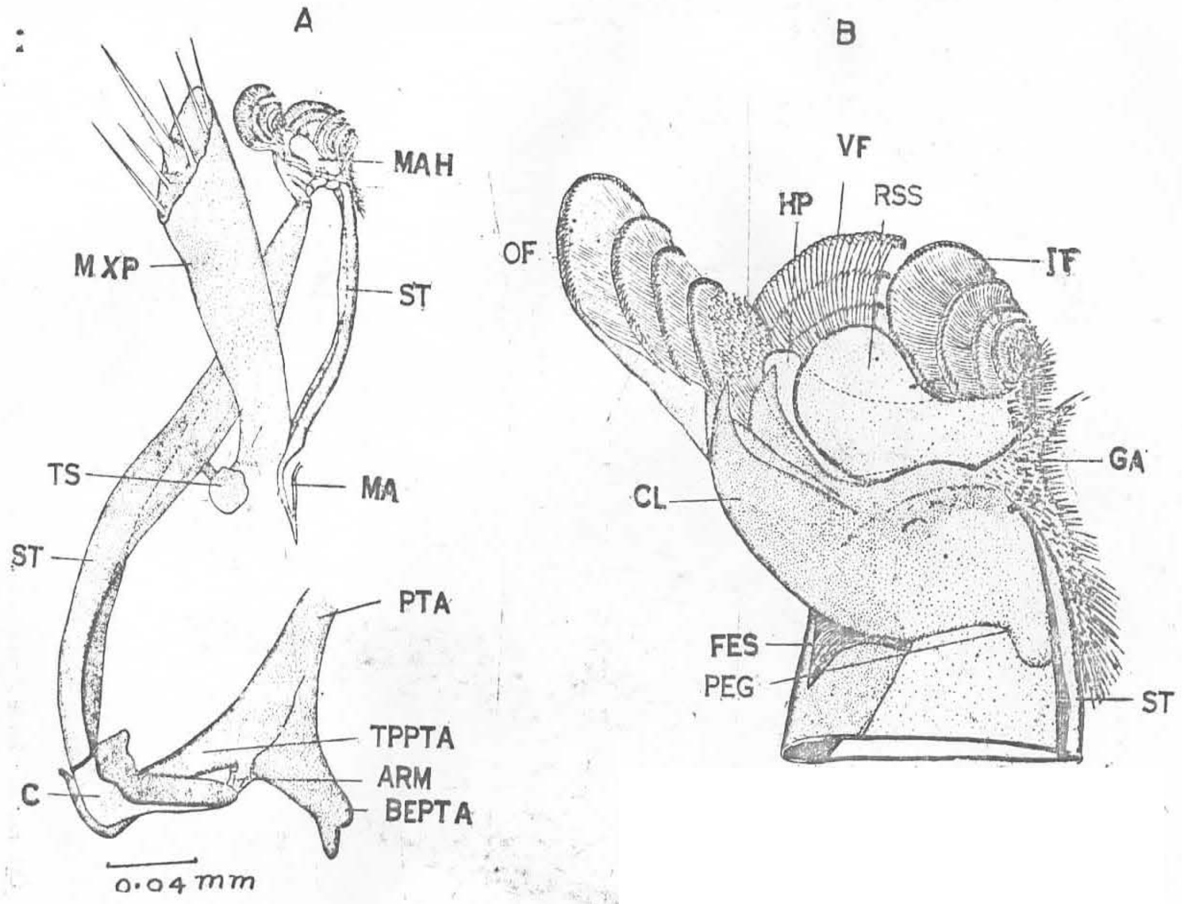

FIG. 4

Fig. 4. Mouthparts of *T. longicornis.*
(*a*) Dorsal view of the right maxilla head.
(*b*) Dorsal view of the right maxilla. A portion of the posterior tentorium has been incorporated to show their relative positions.

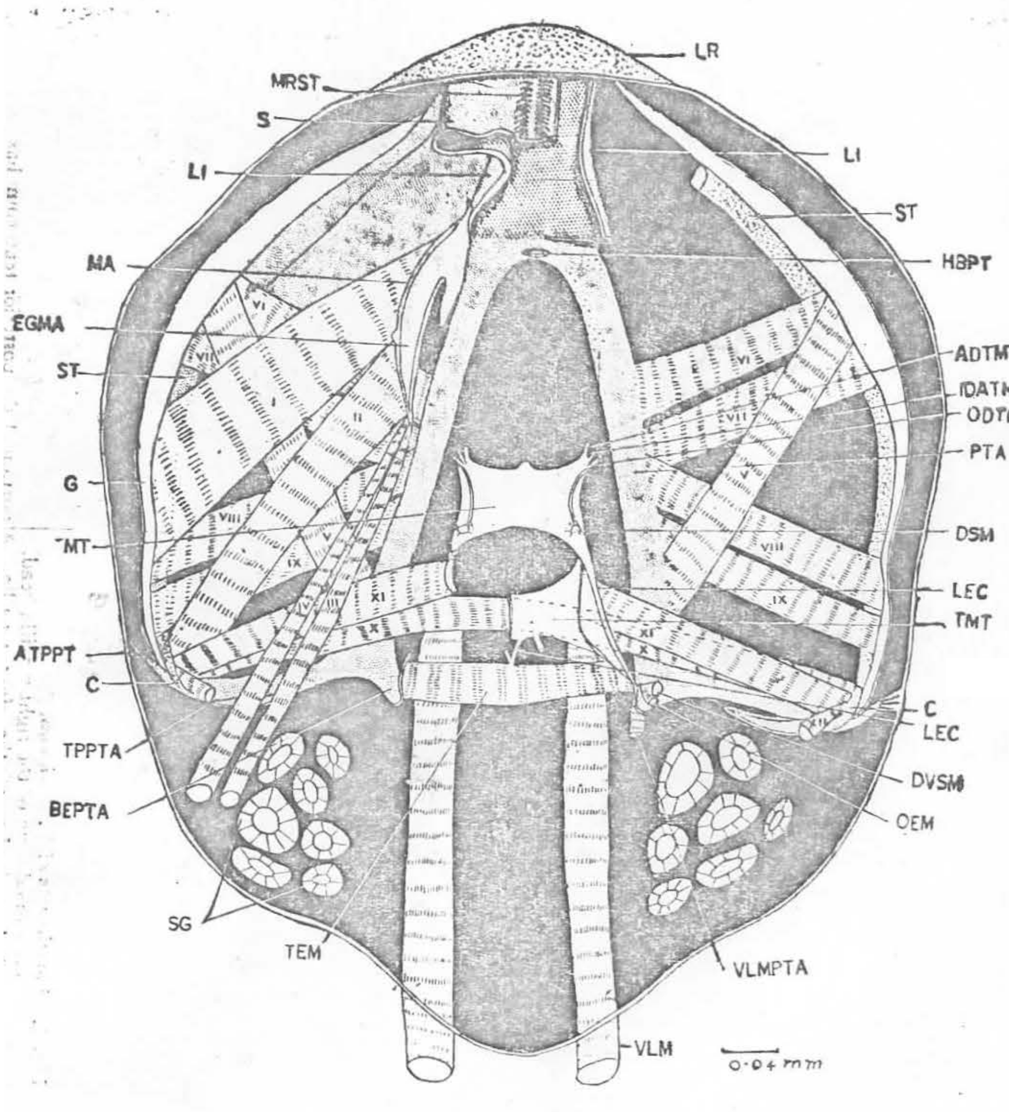

FIG. 5

Fig. 5. Diagramatic horizontal section (reconstructed) of the head of *T. longicornis* showing the maxillary muscles viewed from above. The left side is at a more dorsal level than the right. The endoskeletal structures and the ventral longitudinal muscles have been incorporated in the diagrams although they are at a slightly different level.

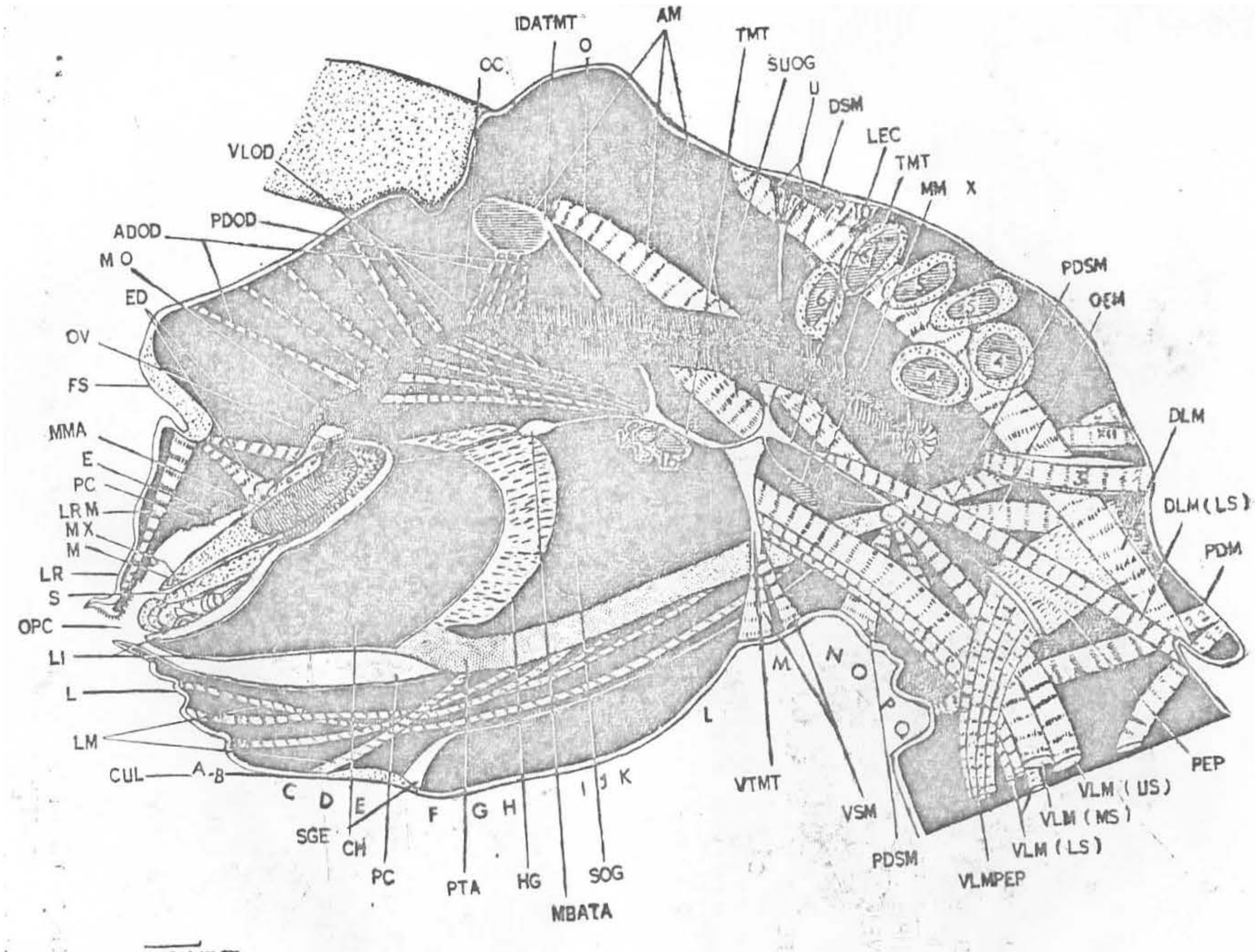

FIG. 6

Fig. 6. Reconstruction of a sagittal half of the head of *T. longicornis* viewed from the mid line. The levels of subsequent transverse sections are marked by letters A-Q.

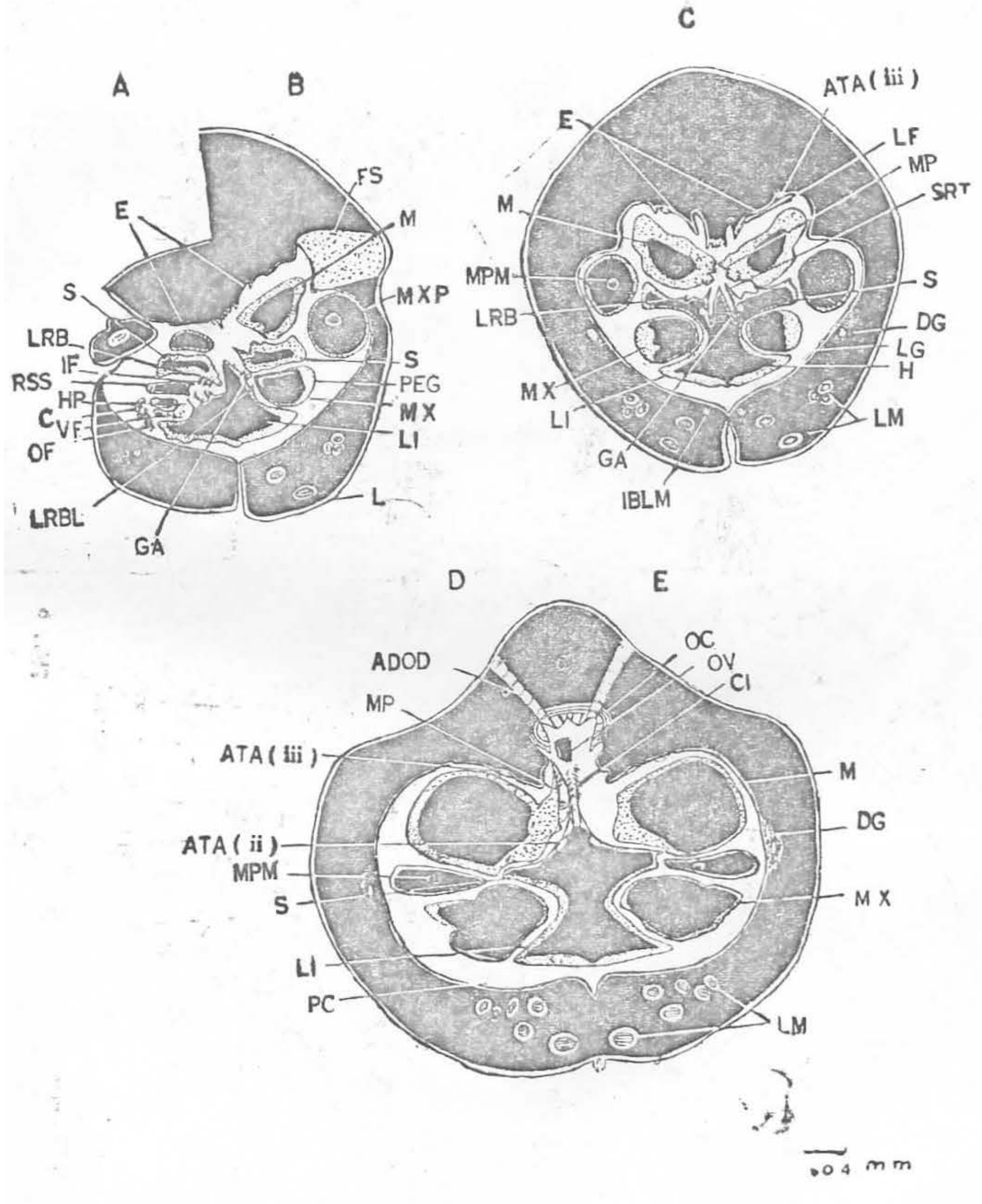

FIG 7

Fig. 7. Diagramatic T. S. of halves of the head of *T. longicornis* passing through levels A, B C, D and E (see Fig. 6).

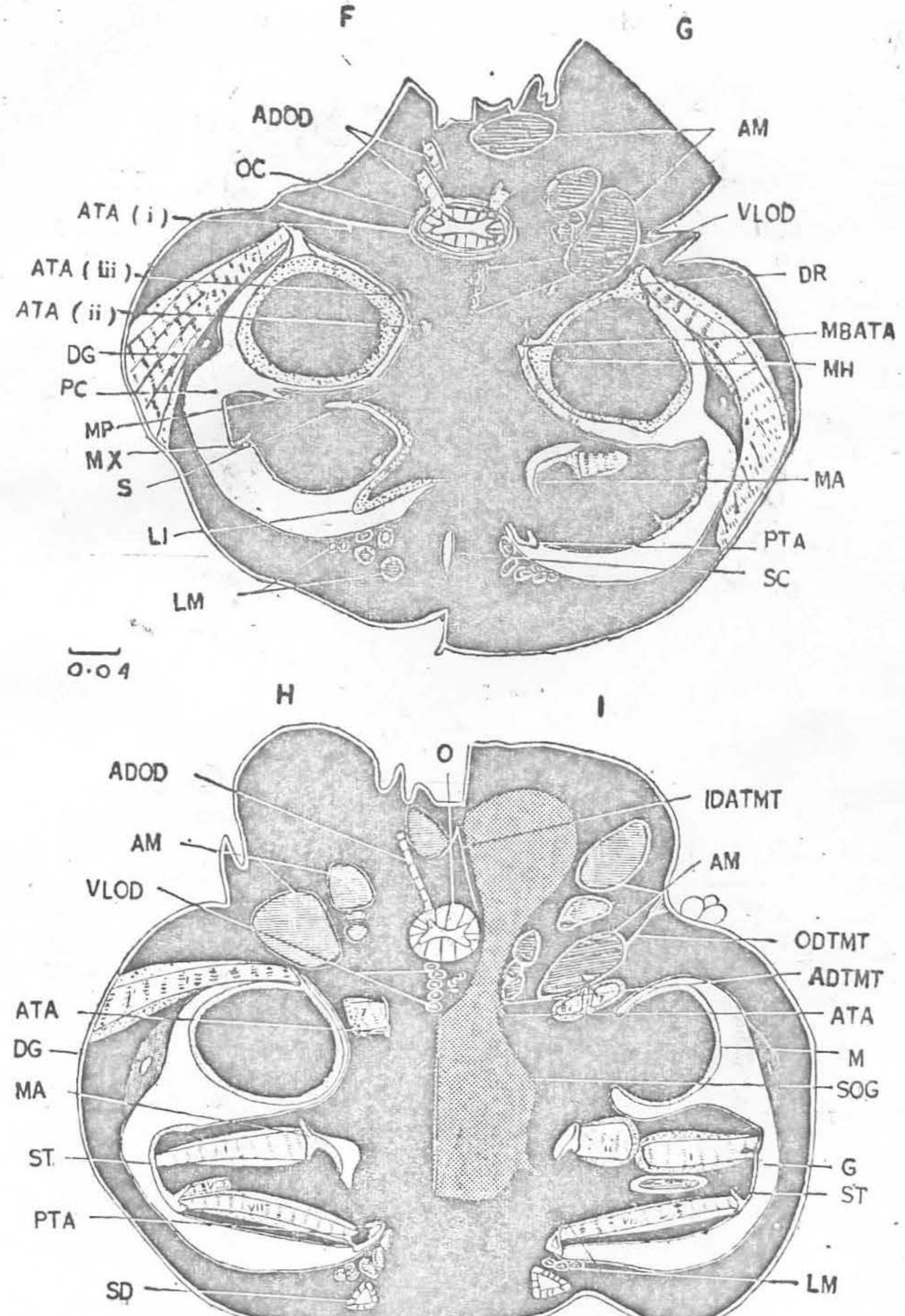

FIG. 8

Fig. 8. Diagramatic T. S. of halves of the head of *T. longicornis* passing through levels F, G, H, and I. (see Fig. 6).

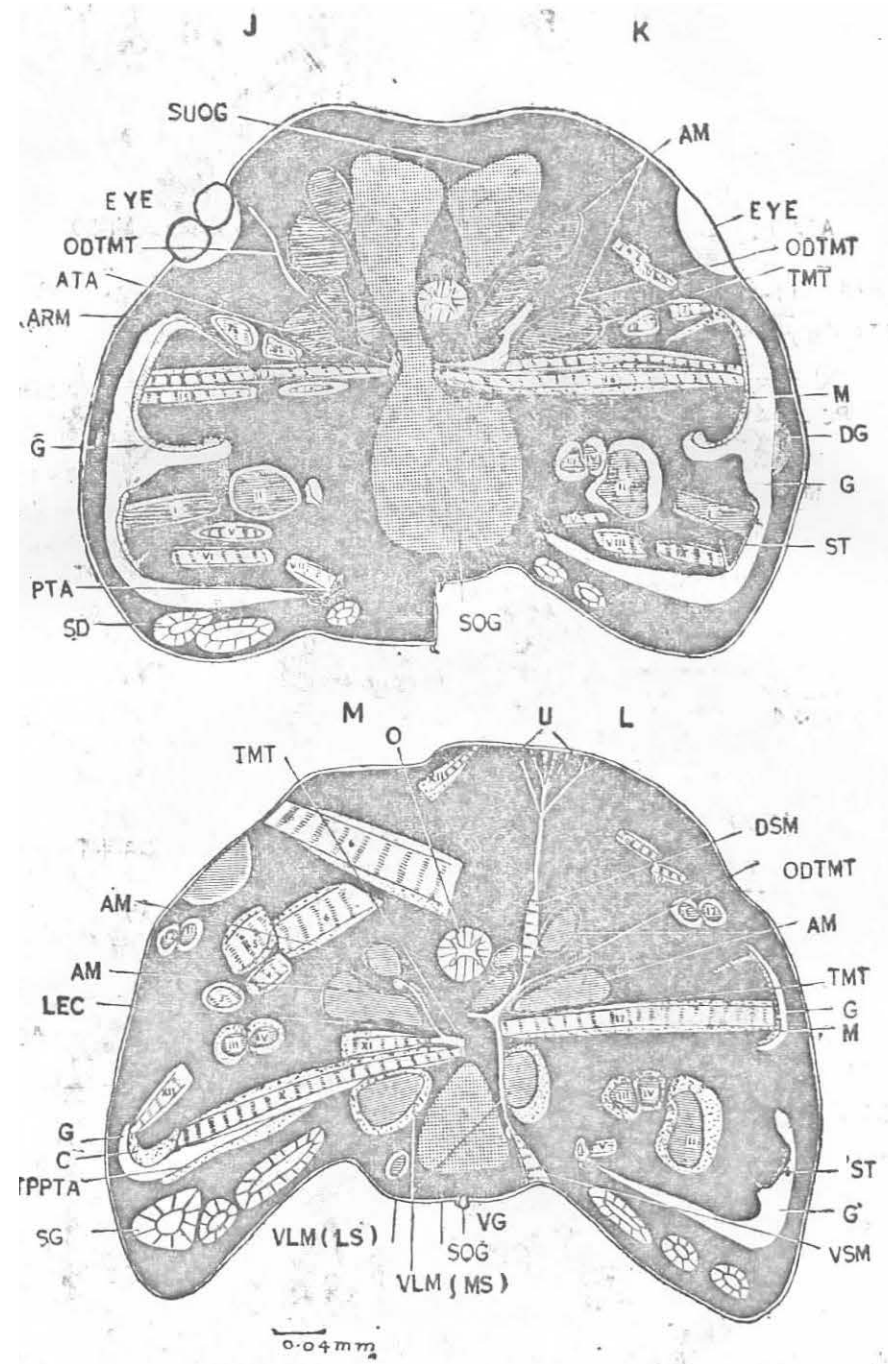

FIG. 9

Fig. 9. Diagramatic T. S. of halves of the head of *T. longicornis* passing through levels J, K, L and M (see Fig. 6).

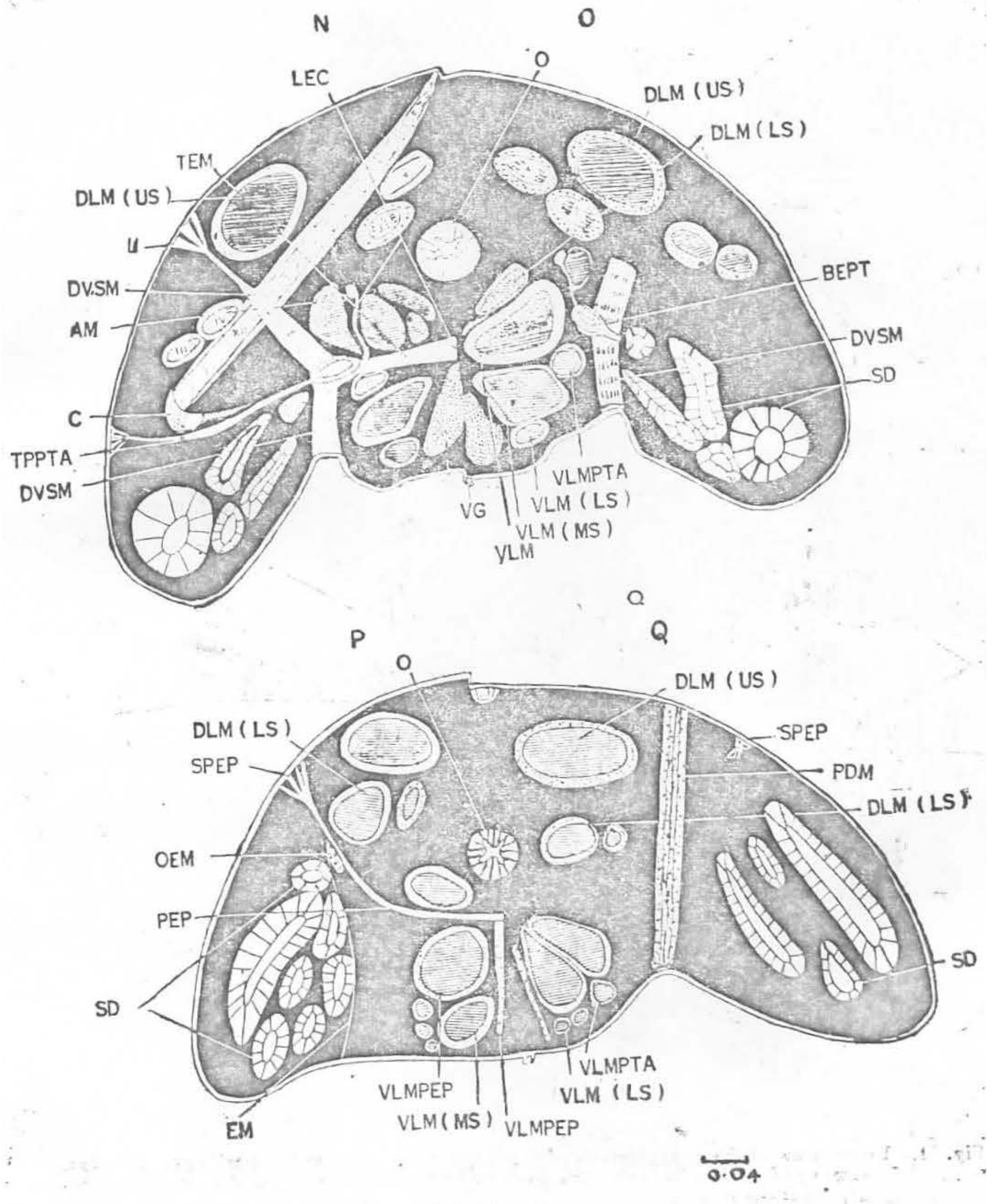

FIG. 10

Fig. 10. Diagramatic T. S. of halves of the head of *T. longicornis* passing through levels N, O, P and Q (see Fig. 6).

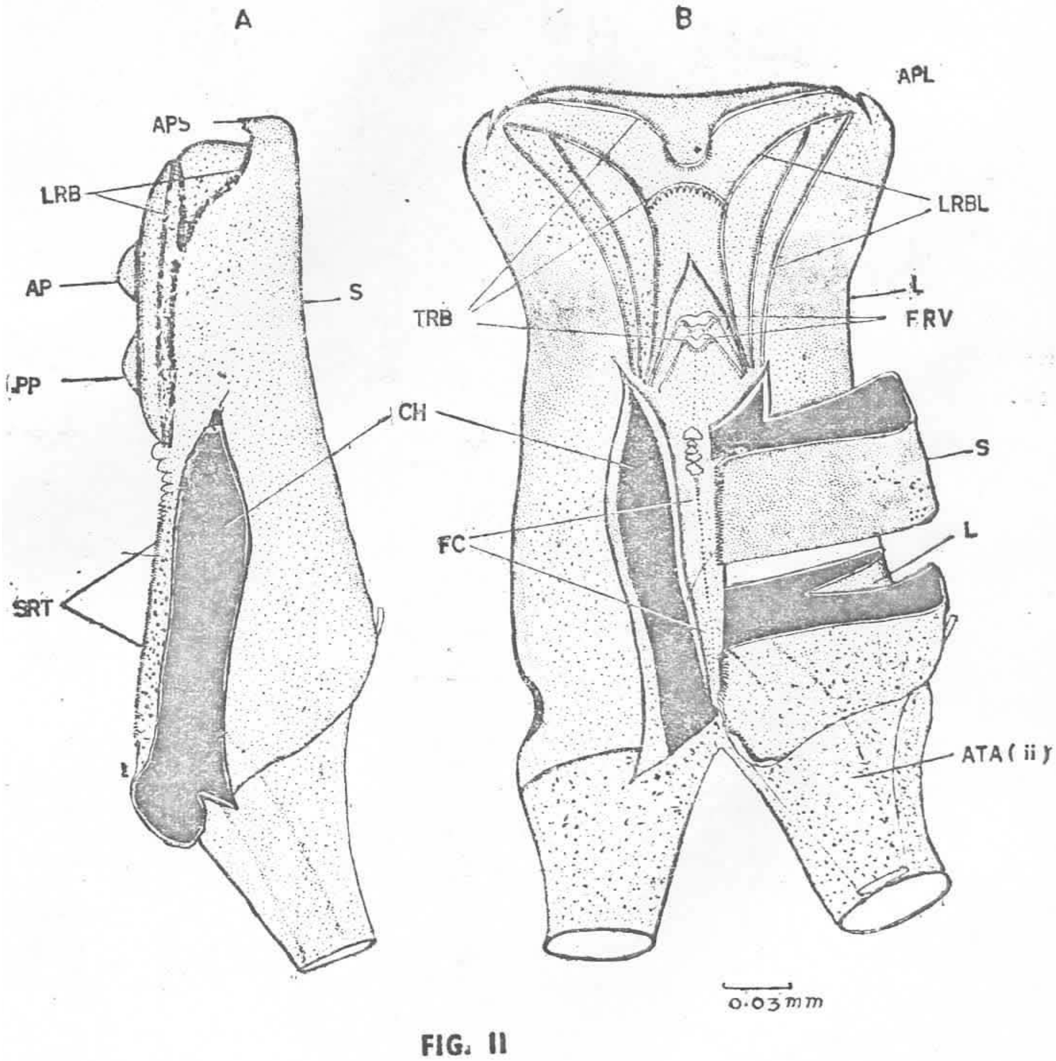

FIG. 11

Fig. 11. Dorsal view of the hypopharynx of *T. longicornis*. The left superlingua has been removed from the hypopharynx to show its ventral aspect and to reveal the dorsal aspect of the lingua.

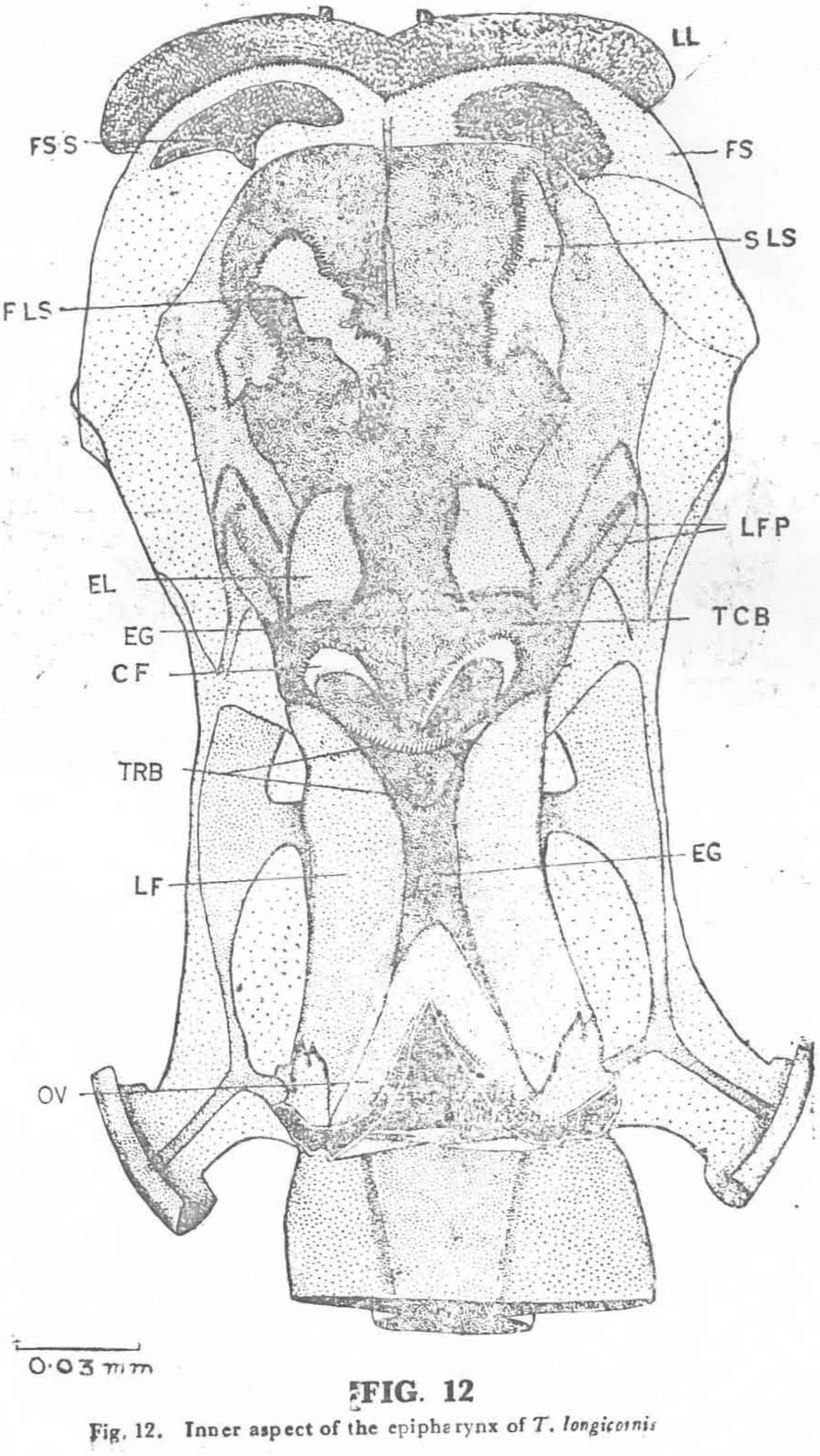

FIG. 12

Fig. 12. Inner aspect of the epipharynx of *T. longicornis*

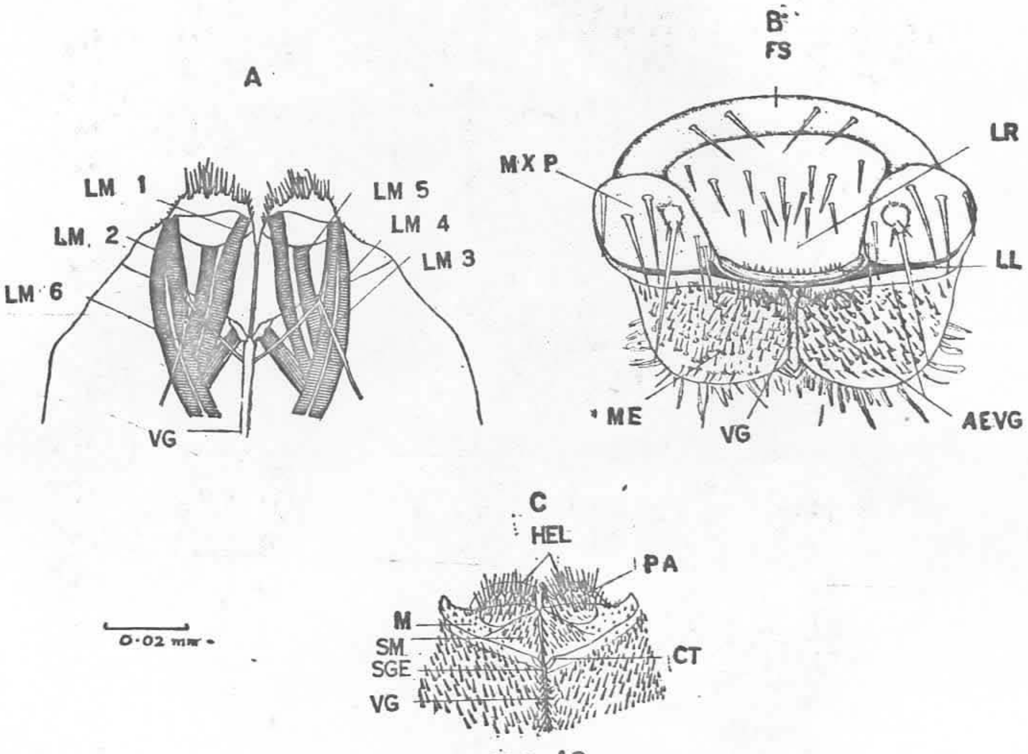

FIG. 13

Fig. 13. Pre-oral cavity and labium of *T. longicornis*
(*a*) External aspect of the opening of the pre-oral cavity.
(*b*) Internal aspect of the musculature of the labium
(*c*) External aspect of the labium.

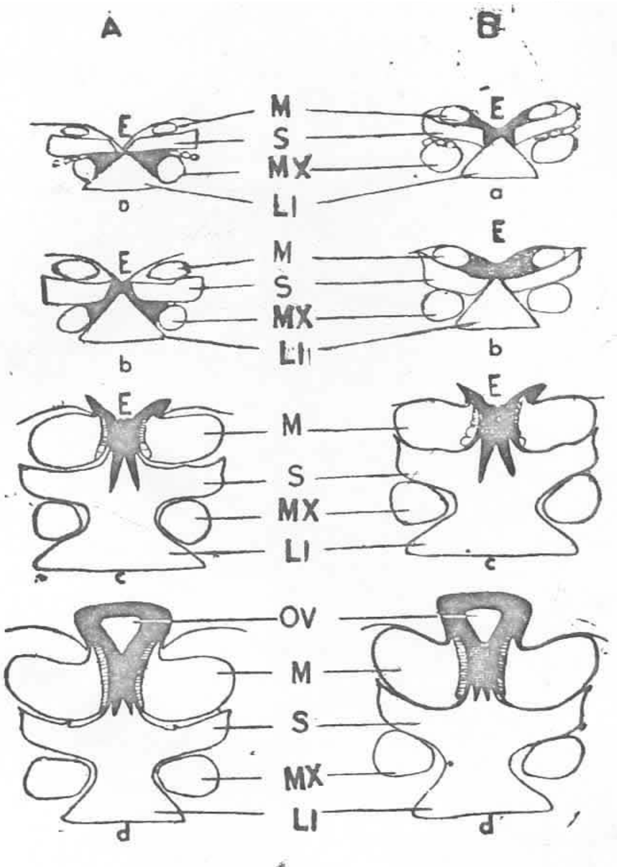

FIG. 14

Fig. 14. Diagrams showing the food meatus in T. S. during feeding of *T. longicornis* on different types of food. The path of the food is stippled.
A.—Solid food.
B.—Fluid food.
(Ep=Epipharynx ; M.=Mandible ; Mx=Maxilla
Sl=Superlingua ; L.=Lingua and Ov=Oral valve.

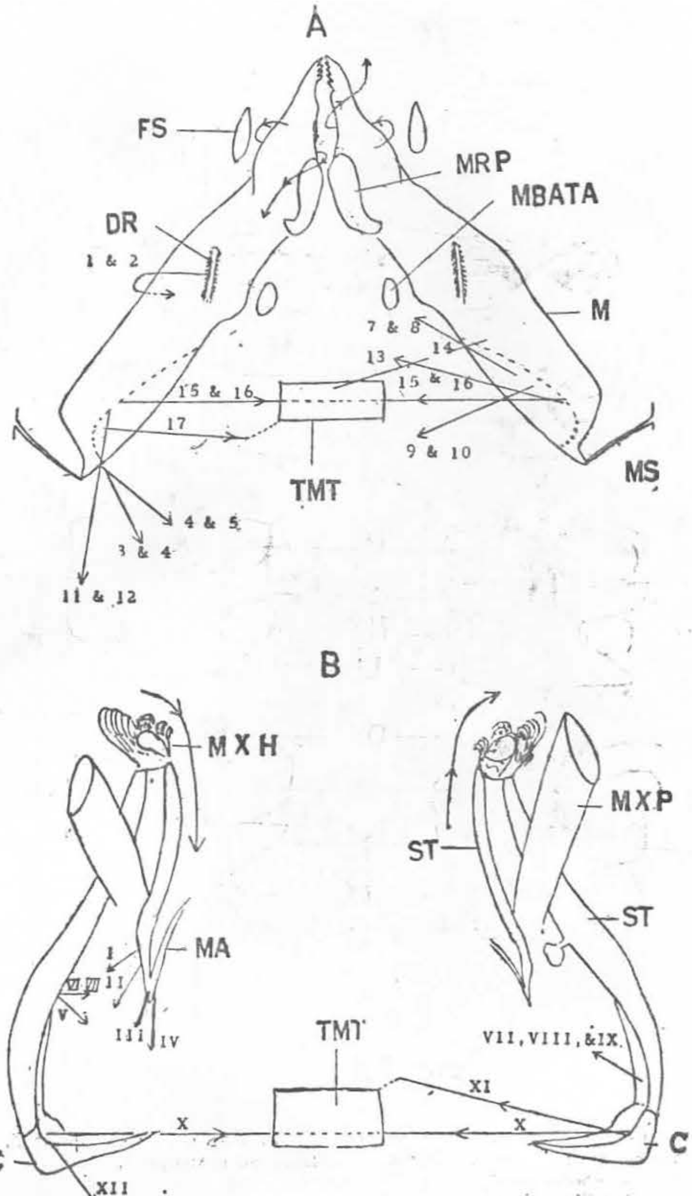

FIG. 15

Fig. 15. (*a*) Diagramatic representation of the mandibular muscles and the movements brought about by them.
(*b*) Diagramatic representation of the maxillary muscles and the movements brought about by them.

EXPLANATION OF FIGURES

A	Antenna.
AM	Antennal muscle.
ADTMT	Anterior dorsal arm of transverse mandibular tendon.
ADOD	Anterior dorso-lateral oesophageal dilators.
AEVG	Anterior end of ventral groove.
AP	Anterior pad.
APL	Anterior promontary of lingua.
APS	Anterior promontary of Superlingua.
ATA (*i*)	Anterior tentorial apodeme (branch-*i*)
(*ii*)	Anterior tentorial apodeme (branch-*ii*)
(*iii*)	Anterior tentorial apodeme (branch-*iii*)
ARM	Arthrodial membrane.
ATPPT	Attachment of transverse process of posterior tentorium.
BEPTA	Blind end of posterior tentorial apodeme
CH	Cavity of Hypopharynx.
C	Cardo.
CT	Chitinous thickening.
CI	Cibarium.
CF	Crescentric flap.
CL	Claw.
CUL	Close union of labium.
D	Diastema.
DR	Dorso-lateral mandibular ridge.
DLM (US)	Dorsal longitudinal muscles (upper sector).
(MS)	Dorsal longitudinal muscles (middle sector).
(LS)	Dorsal longitudinal muscles (lower sector).
DSM	Dorsal suspensory muscle.
DSG	Ductless Salivary gland.
DTB	Dorsal tract of bristles.
DVSM	Dorso-ventral suspensory muscle.
DG	Ductless gland.
E	Epipharynx.
EG	Epipharyngeal groove.
EL	Epipharyngeal lobe.
ED	Epipharyngeal dilators.
EM	Endoskeletal membrane.
EGMA	Extension of gnathalpouch into maxillary apodeme.
FES	Flattened end of stipes.
FLS	Flap like structure.
FC	Floor of cibarium.
FRV	Food retaining valve.
FS	Frontal sclerite.
FSS	Field of small spine.
GA	Galeal appendage.
G	Gnathalpouch.
H	Hypopharynx.
HEL	Hyaline end of labium.
HP	Hyaline plate.
HG	Hypopharyngeal gland.
HBPT	Hypopharyngeal bar of posterior tentorium.
I	Incisor.
IBLM	Inner branch of labial muscle 2.
IDATMT	Inner dorsal arm of transverse mandibular tendon.
IDSM	Inner dorsal suspensory muscle.
IDAMT	Inner dorsal arm of mandibular tendon
IF	Inner fan.
LM	Labial muscles.
LM-1	Labial muscle – 1.
LM-2	Labial muscle – 2.
LM-3	Labial muscle – 3.
LM-4	Labial muscle – 4.
LM-5	Labial muscle – 5.
LM-6	Labial muscle – 6.
L	Labium.
LR	Labrum.
LRM	Labral muscle.
LF	Lateral fold.
LFP	Lateral flap.
LG	Lateral groove.
LL	Lip of labrum.
LI	Lingua.
LEC	Longitudinal Endoskeletal connective.
LRB	Longitudinal rows of bristles.
M	Mandible.
MHK	Mandibular hook.
MC	Mandibular cavity.
MMA	Mandibular molar area.
MH	Mandibular hump.
MS	Mandibular suspension.
MBATA	Mandibular boss on anterior tentorial apodeme.
MA	Maxillary apodeme.
MXP	Maxillary palp.
MPM	Maxillary palp muscle.
MXH	Maxilla head.
MM	Maxillary muscle.
MX	Maxilla.
MN	Mentum.
MGL	Median gap of labium.
MRST	Mesial row of superlingual teeth.
MRP	Molar plate.
MO	Mouth.
OEM	Oblique endoskeletal muscle.
O	Oesophagus.
OC	Oesophageal constrictor muscles.
OPC	Opening of the pre-oral cavity.
OV	Oral valve.
ODTMT	Outer dorsal arm of transverse mandibular tendon.
ODSM	Outer dorsal suspensory muscle.
OF	Outer fan.
OSBS	Oral space between superlinguae.
PDM	Posterior dorso-ventral muscle.

PDSM	Posterior dorso-ventral suspensory muscle.
PDOD	Posterior dorso-lateral oesophageal dilators.
PEP	Posterior endoskeletal plate.
PEG	Posterior extension of galea (Galeal extension).
PP	Posterior pad.
PRS	Posterior ridge of superlingua.
PTA	Posterior tentorial apodeme.
PA	Palp.
PC	Pre-oral cavity.
RCP	Row of chitinous projection.
RT	Rows of teeth.
RSS	Retort shaped structure.
SG	Salivary gland (segmental organ).
SGE	Salivary gland Exit.
SC	Salivary channel.
SD	Salivary duct.
SLS	Saw like structure.
SH	Shaft.
ST	Stipes.
SM	Sub-mentum.
SOG	Sub-oesophageal ganglia.
SUOG	Supra-oesophageal ganglion.
S	Superlingua.
SRT	Superlingual row of teeth.
SPEP	Suspension of posterior endoskelatal plate.
TCB	Transverse chitinous band.
TEM	Transverse endoskeletal muscle.
TMT	Transverse mandibular tendon.
TMT	Transverse maxillary tendon.
TPPTA	Transverse process of posterior tentorial apodeme.
TRB	Transverse rows of bristles.
TS	Transverse sclerite.
TSPTA	Tentorial sclerotisation of posterior tentorial apodeme.
U	Unstriated fibrils.
VTMT	Ventral arm of Transverse madibular tendon.
VF	Ventral fan.
VG	Ventral groove.
VLOD	Ventral lateral osophageal dilators.
VLMPEP	Ventral longitudinal muscle to posterior endoskeletal plate.
VLMPTA	Ventral longitudinal muscle to posterior tentorial apodeme.
VLM	Ventral longitudinal muscle.
VLM(US)	Ventral longitudinal muscles (upper sector).
(MS)	Ventral longitudinal muscles (middle sector).
(LS)	Ventral longitudinal muscles (lower sector).
(AS)	Ventral longitudinal muscles (All sector).
VRBS	Ventral row of bristles on Seperlingua
VRT	Ventral row of teeth.
VSM	Ventral suspensory muscle.

The retraction-rotation movement is brought about by muscles 1, 2, 3, 4, 5, 6, 11, 12 and 17. Mandibular muscles 1 and 2 originate from the lateral head wall and are inserted on the dorso-lateral ridge of the mandible. These muscles are rotators in function. Mandibular muscle 3 (fig. 3) originates from the posterior median head wall and inserts ventrally on the posterior end of the mandible through a thickened arthrodial membrane. This muscle functions both as a retractor and a rotator. Mandidular muscles 4, 5 and 6 originate from the dorsal head wall and insert on the posteroventral end of the mandibular cavity through a thickened arthrodial membrane (fig. 3). Muscles 4, 5, and 6, which originate on the left of the head wall, insert on the right mandible and *vice-versa* so that the two sets of muscles cross the middle line. These muscles function as rotators, but muscle 4 which has a very posterior origin also acts as a retractor. Muscles 11 and 12 originate from the postero-lateral wall of the head and insert on the dorso lateral ridge of the mandibular cavity. These muscles function purely as retractors. The mandibular muscles 17 is also concerned in the retraction movement of the mandible and it originates from the base of the longitudinal endoskeletal connectives (fig. 9). The point of insertion lies on the postero-ventral wall of the mandibular cavity and thus its function is that of a rotator.

The protraction-counter-rotation of the mandible is brought about by muscles 7, 8, 9, 10, 14, 15 and 16. Muscles 7 and 8 originate from the posterior tentorial apodeme immediately behind the mandibular boss and insert on the chitinous bulge on the dorsal inner wall of the mandibular cavity. The contraction of these muscles brings about protraction as well as counter-rotation of the mandible.

Mandibular muscles 9 and 10 originate from the median dorsal head wall (fig. 6) and insert on the dorsal chitinous bulge in the mandibular cavity. The contraction of these muscles causes rotation of mandible in a direction opposite that of muscles 1, 2, 3, 4, 5, 6 and 17. Muscle 13 is a broad muscle originating from the anterior tentorial apodeme (fig. 9) and inserted on the inner lateral wall of the mandibular cavity, dorsal to the point of insertion of muscles 15 and 16. The point of origin of muscle 13 is slightly anterior to the point of its insertion. Hence the contraction of this muscle may cause a very small protraction and also some abduction of the anterior end of the mandibles.

Mandibular muscle 14 originates ventrally from the anterior median point of the transverse mandibular tendon and is inserted on the lateral inner wall of the mandibular cavity on the same level and anterior to the point of insertion of muscle 13 (fig. 3). The origin of muscle 14 is slightly posterior and lower than its insertion, so that the contraction of this muscle will tend to adduct the anterior end of the mandible, but working in unison with muscles 15 and 16 it is used to counteract any excessive abduction effect produced by muscles 15 and 16. This interpretation of the action of muscle 14 disagrees with that of Manton (1964) who regards it as a levator. Mandibular muscles 15 and 16 (figs. 3 and 9) are inserted on the inner lateral wall of the mandibular cavity ventral to the point of insertion of muscle 13. These muscles alone would cause abduction of the anterior ends of the mandibles, but in combination with the other muscles of this group they probably have a stablizing function during the movement of the mandible.

Maxillae : The detailed structure of the maxilla head of *T. longicornis* is shown in fig. 4. The maxilla head is divisible into an inner ventral part, the lacinia, and an outer dorsal part, the galea. The lacinia is modified into three

fans—the inner fan, the ventral fan and the outer fan. The inner fan is fused at its base with a supporting retort-shaped structure, and similarly the ventral fan is fused with its supporting structure, the hyaline plate. The galea is modified dorso-laterally into a claw with these teeth. Mesially it gives rise to a hollow out growth bearing a large number of bristles, called the appendages of the galea. This is possibly used in moving food particles from the lingua into the cibarium. The dorso-mesial part of the galea is produced posteriorly into the cavity of the stipes and is referred to as the galeal extension. The lacinia is immovably fused together at their bases where they form a heavily chitinised ring which is movably articulated with the stipes. The articalation is such that the movement of the maxilla head is restricted to the lateral plane.

The framwork of the body of the maxilla is formed by the stipes. Anteriorly the stipes bears a palp (fig. 4). At the level at which the palp fuses with the stipes, it also fuses laterally with the postero-lateral margin of the hypopharynx. At this point the maxilla and hypopharynx together form the maxillary apodeme (fig. 8) which bears maxillary muscles I to IV. Sections in fig. 8 G to H would reveal that this apodeme is formed from the fusion of the dorsal wall of the stipes with the base of the palp and the posterolateral wall of the super-lingua, Sections taken in a more posterior region show that at the point of fusion of the ventro-mesial wall of the stipes with the lingua in the region marked with an asterik in fig. 8 F, a small chitinous pocket is left which is continuous with the preoral cavity. This is the maxillary apodeme and serves as the point of insertion of maxillary muscles I to IV (fig. 5).

The main movements of the maxillae in *T. longicornis* are those of protraction accompanied by abduction, and retraction associated with adduction. The maxilla can be protruded through the opening of the pre-oral cavity by maxillary muscles VIII, IX. Muscles VIII and IX originate from the transverse maxillary tendon and inserts on the cardo (fig 9 M). These muscles VIII, IX and XI cause protraction accompanied with some abduction of the maxillary head, while muscle which originates from the mid-ventral aspect of the transverse maxillary tendon, inserts on the cardo and is employed as an abductor of the maxilla head. Since the muscle joins with its fellow of opposite side and is loosely fastened to the transverse maxillary tendon by a thin connective tissue fibre, this may also act as a stabilizer (Manton 1964).

The retraction-adduction movement of the maxilla is brought about by muscles I, II, III, IV, V, VI, VII and XII. The point of origin of muscle I lies on the stipes, that of muscles II on the cardo and that of muscles III and IV on the posterior lateral wall of the head. Muscles I, II, III and IV insert on the maxillary apodeme. Muscle I and II are primarily adductors of the maxilla head, whilst III and IV are retractors. As a result of contraction of muscles I, II, III and IV, the maxilla head is also moved towards the median line, while the maxilla is retracted. Muscles V, VI and VII (fig. 5) originate from the posterior tentorial apodeme and insert on the inner lateral wall of the stipes. Muscle V functions as a retractor Muscle VI and VII act as adductors. Muscle XII originates from the median dorsal head region, anterior to the point of origin of the mandibular muscle 3 (fig. 6) and inserts on the dorsal inner wall of the cardo and functions as a retractor.

Hypopharynx. In Collembola, the hypopharynx is well developed and plays an important role in feeding. The general form and structure of the hypopharynx and the cuticular structure associated with it are illustrated in text figure 11.

The hypopharynx is modified according to the nature of the food. In contrast with fluid feeders in which the hypopharynx has a smooth surface devoid of cuticular processes and serving as floor of the food meatus, in *T. longicornis*, which feeds on solid food, the hypopharynx has a complete series of bristles and processes. It is modified for procuring solid and semi-solid food and conducting it back to the mouth. The free dorso-lateral part of the lingua and ventral aspect of superlingua bear three longitudinal tracks of bristles between which the fans of the maxilla head work (fig. 7 A). The longitudinal rows of bristles on the hypopharynx assist in conducting food to the mouth and also prevent the food particles from escaping into the lateral groove (fig. 7*c*). Posteriorly they are continued as transverse rows of bristles so that the food, brushed along the longitudinal and transverse rows of bristles on hypopharynx, comes to lie in a narrow space at the anterior end of the cibarium. The transverse rows of bristles appear to prevent the food from moving anteriorly, which function is also performed by the 4th and 5th transverse rows of bristles which are borne along the mid line on a raised area and are directed posteriorly. The latter are food retaining valve (fig. 5) The superlinguae bear on their dorsal surfaces, one longitudinal track of bristles which serve to prevent the food particles escaping dorsolaterally across the surface of the superlingua into the pre-oral cavity in the region of the mandibular diastema. The superlingue are lobed on their median surface forming two pairs of distinct pads. The function of the pads and the lobed margins of the superlinguae is possibly to prevent the food particles from escaping dorsally across the superlingue.

The posterior part of each superlingua is fused ventrally to the postero-dorsal surface of the lingua in such a way that the median dorsal surface of the lingua continues posteriorly as the floor of the food meatus or cibarium. The sides and the roof of the cibarium are formed by the arching of the toothed mesial edges of the superlinguae which assist in the food being picked up between the molar plates during rotation-retraction movement. The cibarium opens anteriorly opposite the oval space between the superlinguae while posteriorly this groove is raised and forms a triangular oral valve (fig. 6) which lies in front of the mouth. The base of the oral valve lies dorsally and is continuous posteriorly with the ventral wall of the oesophagus while the two sides are formed by the cibarium. It acts as a door, opening the passage to the mouth only when the mandible is rotating. The hypopharynx is devoid of any muscle of its own. The movement of the lingua and the superlinguae is brought about by the movement of the anterior and posterior tentorial apodemes.

Buccal cone, pre-oral cavity and oesophagus. The conical hypostome is bounded dorsally by the labrum and ventrally by the labium and encloses a space between them known as the pre-oral cavity. In repose, the mouth parts are concealed in the pre-oral cavity and the slit-like opening of the pre-oral cavity is tightly closed by the labrum and labium. (fig. 13*a*)

The labrum is an unpaired quadrate leaf-like structure, broader at the base than at the apex. Longitudinal sections show that the edge of the labrum, proximal to its attachment with the frontal sclerite, becomes slightly invaginated to form a sigmoid ridge of thick elastic cuticle, referred to as the fronto-labral suture. The fronto-labral suture provides sufficient elasticity to allow return of the labium to its original position during relaxation of the labral muscles. This mechanism explains the absence of elevator muscles in the labrum. This fronto-labial suture is at the base of the hypostome in *T. longicornis* (fig. 6). The dorsal surface of the labrum bears a number of suitable bristles believed to be sensory in nature. The distal margin of the lip of the labrum, the structure of which is

correlated with the feeding habit of the species in question, is semi-circular, stiff and provided with a large number of minute, backwardly directed bristles in this species feeding on solid moist food. It helps in conducting food particles into the pre-oral cavity (fig. 13).

A pair of labral muscles originates from the fronto-labral sutures and inserts on the distal end of the labrum (fig. 6). These muscles help to depress the labium. At its tip, the labrum continues backwards and inwards as the epipharynx (fig. 6 and 12) which forms the roof of the pre-oral cavity. The epipharynx can be divided into two regions—the anterior region bears the assymetrical saw-like and flap-like structures and the posterior region bears the lateral folds. The anterior region is wedge-shaped in transverse sections (fig. 16 A, B) so that when it meets the median dorsal part of the lingua, it divides the food meatus into two lateral channels. The wedge-shaped structure of the pharynx extends posteriorly to a point above the food retaining valve on the lingua. Posterior to this point, the epipharynx gradually becomes concave and bears lateral folds in the region where it lies dorsal to the madibular molar plate. Posteriorly, the epipharynx encloses the oral valve (fig. 16 D). The various chitinous structures borne by the epipharynx in *T. longicornis* are illustrated in fig. 12. These chitinous structures keep the food particles confined to the food meatus.

There are two pairs of epipharyngeal dilators (fig. 6). These insert on the epipharynx and originate from the fronto-lateral sutures and their contraction creates a negative pressure. The oesphageal muscles consist of the dorso-lateral oesophageal dilators which are divided into two groups—six pairs of anterior and four pairs of posterior dorso-lateral oesophageal dilators. The origin and insertion of these muscles and also the manner of their attachement are illustrated in text figures 6, 7 and 8. By contracting, these muscles pull up the roof of the oesopharynx whereas its floor is pulled down by another set of five pairs of muscles, the ventro-lateral oesophageal dilators. Thus these muscles can create a negative pressure in the oesophagus. The contraction of the oesophagus is brought about by constrictor muscles (fig. 6).

The structure of the labium is illustrated in the text figure 13 *b*, *c*. Subulate sensory bristles are found on the outer surface of the labium. The labial muscles in *T. longicornis* are stouter than in the fluid feeders (Singh 64*a*). There are six pairs of these, four pairs of elevators and two pairs of depressors. The labial musculature resembles that of *T. plumbeus*, described by Hoffmann (1908), whose sequence of numbering has, therefore, been adapted

The labial muscle 1 originates from the posterior tentorial apodeme and is inserted at the inner anterior end of the mentum through the inter mediary of a ligament which is itself attached to the chitin by fibrils. Muscle 2 is formed by the union of two diverging branches a longer and thinner branch. originating from the posterior tentorium and a shorter and thicker branch originating near the point of insertion of muscle 6 of the postero-mesial end of the submentum. Both these diverging branches join at the level of the posterior margin of the submentum and insert on the antero-lateral angle of the mentum, mesial to muscle 3. The points of origin of muscles 3 and 4 lie on the posterior tentorial apodeme and their points of insertions on the lateral inner part of the mentum. Labial muscle 5 also takes its origin from the posterior tentorial apodeme but inserts on the median posterior end of the mentum. Labial muscle 6 which is the posterior most, strongest and shortest labial muscle also originates from the posterior tentorial apodeme and is inserted on the posterior side of the median chitinous thickenning. It is interesting to note that three of the muscles are inserted close

together while one *viz.* 1, is inserted mesially alone on the anterior angle of the labium. Possibly the effect produced by these muscles results in the formation of a concave inner labial surface for scooping. The contraction of muscles 5 and 6 will depress the labium and also restrict the protrusion of the anterior end of the posterior tentorial apodeme and, thereby, the hypopharynx. It also acts as a pivot for raising the anterior end of the hypopharynx. These muscles would move the labial palp dorso-ventrally, causing downward movement of the bristles of the palp.

Feeding machanism

An account can now be given of the method of feeding in *T. longicornis* on the basis of the detailed anatomy of the mouthparts and their musculature, movements of the mouthparts as observed in living animals and experiments to show the path followed by food.

T. longicornis feeds mainly on moist solid food particles but is also capable of feeding on fluid food materials (Singh, 1964*b*).

Whilst feeding on solid food, the hypostome is directed against the food and the mouthparts are then protruded through the opening of the pre-oral cavity, which is widened by lowering the labium and raising the labrum. During this process the tips of the mandibles and maxillae diverge, as they emerge from the opening of the pre-oral cavity, until they are fully separated on the food surface. At the same time, the hypopharynx is also slightly protruded. As soon as the mouthparts touch the food surface, the protraction, which is also accompanied by a counter-rotation movement of mandibles, stops and the various mouthparts take up their operative positions. The first incisor tooth of the mandible pierces the food and its length limits the depth of the scraping, while the remaining incisors, with their tips facing ventro-mesially, grip the food and are ready to scrape the surface during the rotation-retraction movement.

The maxilla heads, lying ventro-lateral to the mandible and the superlinguae, remain on the food with their inner fans facing ventro-mesially, the ventral fan lying laterally and the outer fan more dorsal in position. The hypopharynx and the labium are pressed against the food from beneath in the median line, whilst the labrum presses the food with its distal row of bristles from above. When this arrangement of the mouthparts on the food is completed at the end of protraction, a rotation-retraction movement starts. At the commencement of the rotation-retraction movement the incisors begin to move towards the median side and at the same time retract into the pre-oral cavity, cutting and scraping the soft food (fungal hyphae and spores) as they do so. The mandibles are brought closer together as they move backward, and with them a portion of the food which they scrape may also be moved in the median line and is brought on the tip of the lingua lying below and near the food. Following the retraction of the mandibles, the maxillae begin to move mesially and backward, sweeping the rest of the food on to the tip of the lingua with the help of the fans. During this movement, the maxilla head is slightly rotated so that the outer fan now comes to lie laterally before entering the pre-oral cavity. The function of the outer fan is to prevent stray fungal elements entering the opening of the pre-oral cavity laterally.

As the maxilla head is in the process of retraction, the hypopharynx and the labium are pressed against the food and also raised in order to scoop the food brought between and in front of them by the mandibles and maxillae. The distal backwardly directed bristles on the tip of the labrum are lowered and pressed as the mouthparts and hypopharynx with the food between them are retracted backward into the pre-oral cavity.

In this way the food materials which have been cut and scraped by the mandibles are brought inside the pre-oral cavity with the help of the hypopharynx, mandibles and maxillae, all working slightly out of phase with each other. When the mandible, maxillae and hypopharynx are sufficiently retracted inside the pre-oral cavity, the external opening is closed by the approximation of the labium and labrum. As a result of the lowering of the labrum, the wedge-shaped anterior portion of the epipharynx hangs vertically downward above the lingua so that the food meatus at this end is divided longitudinally into two lateral halves. In each half of the food meatus the maxilla head rushes the food backward in the pre-oral cavity. The food now lies along the dorso-lateral sides of the wedge-shaped lingua between the maxilla heads and superlinguae and below the epipharynx. In the pre-oral cavity the retraction of the hypopharynx ceases but that of the maxillae and mandibles continues for some distance. The fans of the maxillae lie between the lingua and superlinguae in such a way that the free part of their bristles work in close association with the rows of bristles on the lingua and superlinguae. After the movement of the hypopharynx has ceased, and while the maxillae continue to retract, the free margins of the inner and ventral fans sweep the food particles along the longitudinal rows of bristles on the lingua and superlinguae, and deposit them at the posterior end of the lingua.

During the passage of the food from the distal end of the lingua to the posterior end, the anterior and posterior pads, and a median ridge of the epipharynx also prevent the food from escaping dorsally between the superlingua and epipharynx. The food deposited at the posterior end of the lingua is pushed back into the cibarium by the galeal appendages of the maxillae (figs. 4 and 6). The food which has been pushed into the anterior end of the cibarium remains on the floor of the cibarium during the subsequent protraction movement of the mandibles and maxillae but when retraction and rotation of the mandibles commences once more, it is picked up between the rotating medibular molar plates, as they pass the rows of superlingual teeth. All the food particles above the cibarium are thus taken up between the rotating mandibles which, in so doing, also comminute them. During the rotation movement, the epipharynx is applied dorsally to the molar plate so that the anteriorly directed bristles of the crescentric flap prevent any ground up food escaping antero-dorsally.

As the rotation continues, the mandibular hook (fig. 2) pushes the lateral folds apart so that a narrow gap remains between them and the oral valve. The food particles are sucked in through the opening between the lateral folds and the oral valve into the oesophagus. The food from the oesophagus is forced into the gut by the contraction of the constrictor muscles.

Although the usual food of *T. longicornis* is of a solid or semisolid nature, it can also feed on fluid food. The hypopharynx is greatly modified for feeding on solid food particles but it can also be employed in fluid feeding. A functional watertight sucking tube is formed in the pre-oral cavity by sealing the sides of the food meatus (fig. 14*B*). The roof of this tube is formed by the epipharynx and the floor by the lingua. The outer edges of the superlinguae are pressed against the epipharynx and the inner edges are in contact with the body of the lingua. During fluid feeding, the superlinguae are at an angle to their usual position. This is brought about by pressure from beneath, exerted by the maxillae heads. In this way a rather sort of tube is formed which, however, is sufficiently watertight to allow fluid feeding.

In the region of the mandibular molarplate the lateral edges of the superlinguae are raised by the maxilla. The superlinguae are pressed against the

mandibles and thus seal the space between them. The lateral folds of the epipharynx prevent the escape of fluid dorso-laterally above the molar plates and in this way seal the space between the epipharynx and the mandibles and open the passage between the lateral folds and the oral valve. The tip of the water-tight tube is formed by hypopharynx below and the labrum above. This is dipped into the food and the fluid is sucked into the pre-oral cavity by the negative pressure created by the action of the epipharyngeal and oesophageal dilator muscles. The mandibles and maxillae remain immobile during fluid feeding.

Summary

The detailed anatomy and arrangement of the mouthparts of *T. longicornis* has been described. The mouthparts are of the biting and scraping type, with well developed mandibular molar plates and complex maxillary heads. Arrangements of mandibular and maxillary muscles are similar to those described by Hoffmann (1905 and 1908) and Manton (1964). The structure of the hypopharynx and the hitherto unknown tongue-like oral valve has been fully described and their relationship with feeding mechanism discussed. The complex epipharynx is wedge-shaped anteriorly where it divides the food meatus into two lateral channels while posteriorly it forms the arched roof of the food meatus. Solid food particles are swept along the lateral channels between the lingua and superlinguae by the fans of the maxillary heads and finally deposited before the entrance of the cibarium. After further protraction movement, food is picked up from the floor of the cibarium by the mandibular molar plates which grind and carry it dorsally to the opening of the mouth, from where it is sucked into the oesophagus through the oral valve due to the negative pressure created inside the oesophagus. For feeding on fluid food, a functional tube is formed between the lingua, superlinguae, and epipharynx. Through this improvised functional tube, fluid food is sucked into the oesophagus by the negative pressure created by the oesophageal dilator muscles.

Acknowledgements

The author is grateful to the late Professor T. A. Stephenson, D.Sc., F. R. S., and Professor B. M. Jones, D.Sc., Department of Zoology, University College of Wales, Aberystwyth, U. K., for providing laboratory facilities and to Dr. T. B. Poole for supervising the work and Dr. U. S. Srivastava, Professor of Zoology, University of Bihar, Muzaffarpur, for going through the manuscript.

The author would also like to express his gratitude to Dr. S. M. Manton, F. R. S. for allowing him to consult the then unpublished manuscript of her paper (Manton, 1964)

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